

**STREPSIPTERA DO NOT SHARE HIND WING VENATIONAL
SYNAPOMORPHIES WITH COLEOPTERAS
A REPLY TO KUKALOVÁ-PECK AND LAWRENCE¹**

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Abstract.—Kukalová-Peck (1991) and Kukalová-Peck and Lawrence (1993) proposed new characters to support a sister-group relationship between Strepsiptera and Coleoptera based on hind wing venation. Through the use of scanning electron microscopy (SEM) and light microscopy, we have examined these putative synapomorphies in multiple strepsipteran taxa and find discrepancies between the author's presentation of strepsipteran venation and those veins we could observe on the specimens themselves. We find that most of the authors' putative synapomorphies are defined imprecisely and do not consist of discrete character states. While the authors have expressed their results in cladistic terminology, they have failed to use standard cladistic methodology in character evaluation. We object to the authors' use of hypothetical groundplans for defining synapomorphy prior to formal cladistic analysis, the heavy reliance on evolutionary scenarios in phylogenetic inference, the lack of adequate outgroup comparison, and the absence of a simultaneous parsimony analysis of the character data. Based on observational discrepancies and methodological improprieties, we conclude that the authors' putative synapomorphies as currently constituted provide no evidence to support a sister-group relationship between Strepsiptera and Coleoptera.

Kukalová-Peck (1991) proposed new synapomorphies for Strepsiptera and Coleoptera based on hind wing venational characters. These characters were later revised, expanded, and presented in more detail in Kukalová-Peck and Lawrence (1993). Previous to this work, there has only been one character supporting a Coleoptera-Strepsiptera sister-group which has survived scrutiny: the ability to power flight with the hind wings (Kinzelbach, 1971, 1990; Kathirithamby, 1989; Kristensen, 1991). Because the phylogenetic position of Strepsiptera has remained one of the most controversial questions in insect ordinal phylogenetics (Kristensen, 1991), and few characters have been found for its placement among the insect orders, these putative synapomorphies are important and deserve closer scrutiny.

The thrust of Kukalová-Peck and Lawrence's work was towards deciphering the phylogeny of Coleoptera using hind wing venation. They examined 200 specimens from 108 families of Coleoptera and three species of Strepsiptera—*Mengenilla* sp., *Cortiophagus rieki*, and *Lychnocolax* sp.—though the actual specimen number was

¹ This manuscript was originally submitted to the Canadian Entomologist in June, 1994; the journal in which the Kukalová-Peck and Lawrence (1993) paper appeared. Due to unacceptably long delays required to get a final review of this manuscript and await a response from Kukalová-Peck prior to publication, it was subsequently withdrawn.

not mentioned. While the authors' putative synapomorphies should be carefully evaluated in the Coleoptera, Strepsiptera, and appropriate outgroups, we will restrict our specific criticisms to their presence and distribution in Strepsiptera. This is because synapomorphies are statements of shared, derived character state distributions. If it can be demonstrated that a certain character is unobservable or undefinable in the Strepsiptera, then regardless of its occurrence in Coleoptera, there is sufficient reason to reject it as evidence supporting a sister-group relationship between Strepsiptera and Coleoptera.

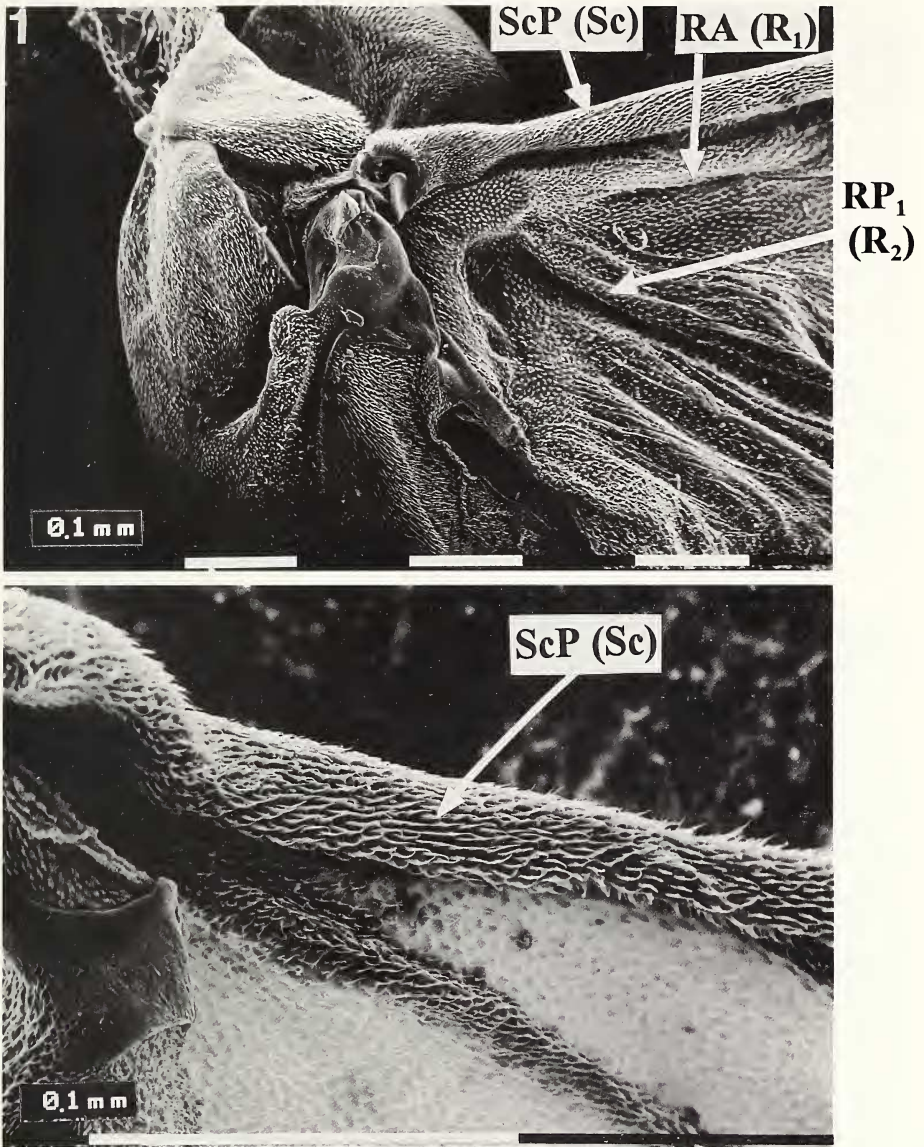
CHARACTER CRITICISMS

We use the following criteria to evaluate Kukalová-Peck and Lawrence's putative synapomorphies: (1) precision of character and state definition e.g., relative size, position, fine structure; (2) whether the states can be defined discretely; (3) distribution of states throughout ingroup taxa; (4) observability of character states in extinct or extant taxa. We agree with Hennig (1966) that only synapomorphy constitutes evidence for monophyly and that symplesiomorphy is phylogenetically uninformative. We further concur with Farris (1990) that non-discrete characters are of little use in phylogenetic analysis because states cannot be objectively defined and state transformations cannot be unambiguously specified. We are therefore concerned that every venational character be defined in such a way as to make the determination of states objective when observing veins on specimens. We further insist that the states be observable in the taxa themselves because inferred states based on preconceived notions of venational evolution in hypothetical prototypes do not constitute *prima facie* evidence for phylogenetic inference.

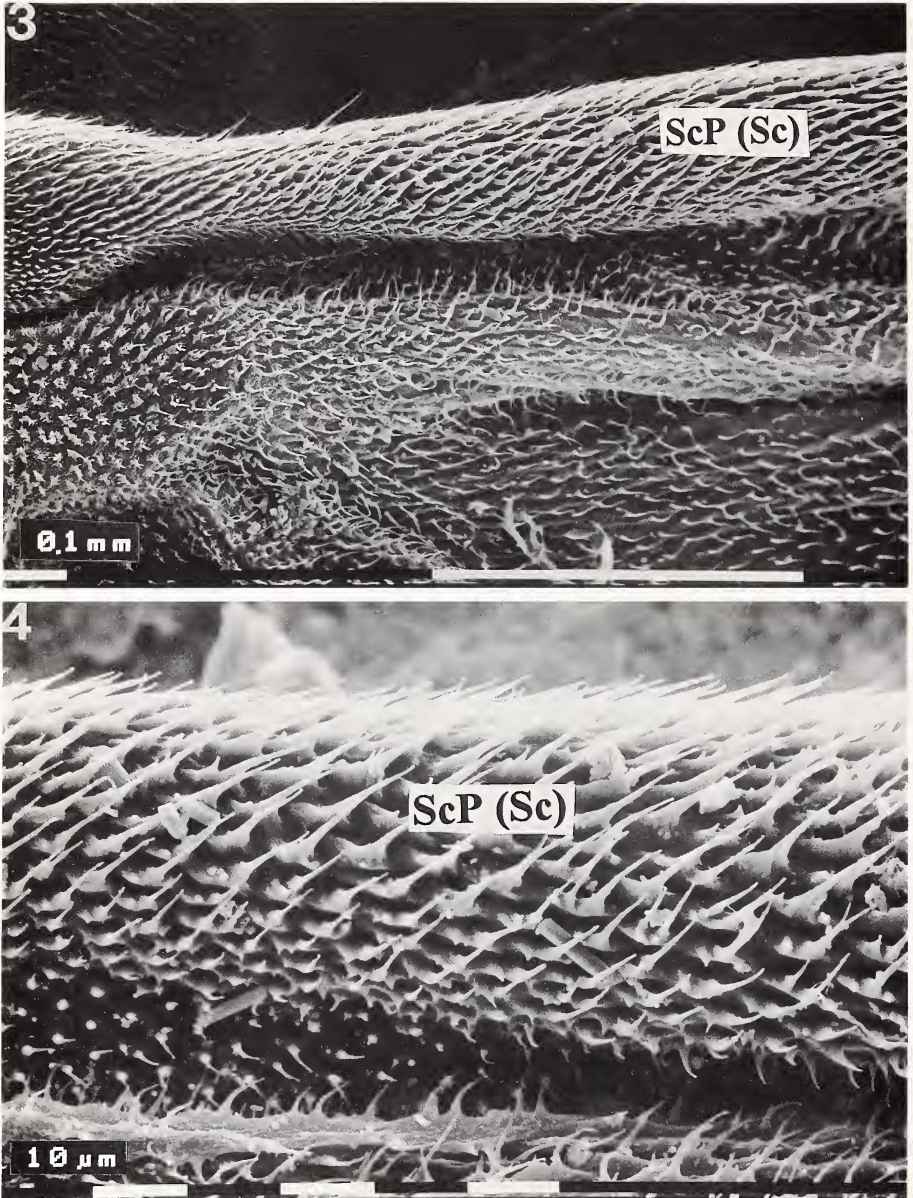
We first provide specific evaluations for each synapomorphy presented by Kukalová-Peck (1991) and Kukalová-Peck and Lawrence (1993). Quotations of original character descriptions (in italics) are followed by the authors' polarity designation. If the same character occurs in both publications, we include both descriptions and polarity designations. Then we evaluate the character and attempt to interpret the states based on the descriptions of the authors. This is followed by specific criticisms of the character and its distribution in Strepsiptera.

Character 1: *A sclerotised and shortened ScP entering the pterostigma* (Kukalová-Peck, 1991; synapomorphy); *ScP ending after entering the pterostigma/radial cell* (Kukalová-Peck and Lawrence, 1993; synapomorphy).

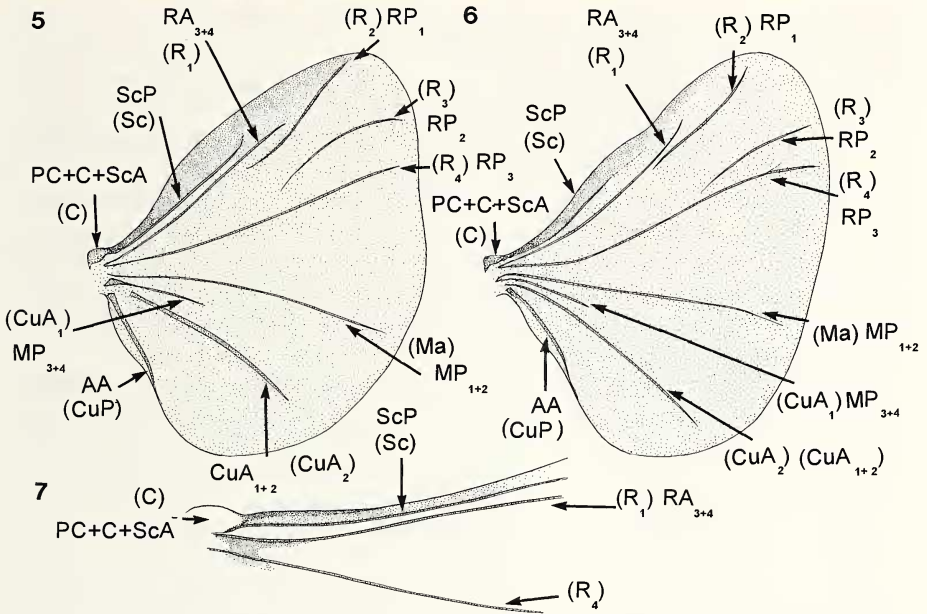
Interpretation: Kukalová-Peck and Lawrence treat C and Sc of Kinzelbach (1971) (Figs. 1–4) as two discrete veins: PC+C+ScA and ScP. According to the authors, ScP runs parallel to the anterior margin of RA and ends abruptly beyond the middle of the wing after entering the pterostigma in Strepsiptera and Coleoptera. They diagrammed PC+C+ScA and ScP as distinct veins visible in the mesothoracic wings of *Mengenilla*, *Coriophagus*, and *Lychnocolax* (Kukalová-Peck and Lawrence, 1993: figs. 69–71). In the authors' drawings of *Mengenilla* and *Coriophagus*, ScP runs into the strepsipteran "pterostigma" (the darkened region between RA₁₊₂ and RA₃₊₄); in the figure of *Lychnocolax* ScP is present but the pterostigma is absent. According to the authors' brief description, the two states of this character are "ScP ending before entering the pterostigma" (plesiomorphy) and "ScP ending after entering the pterostigma" (apomorphy).



Figs. 1–2. SEM of strepsipteran metathoracic wings. Fig. 1 *Coriophagus rieki* Kinzelbach (Halictophagidae), wing base; Fig. 2 *Lychnocolax drysdalensis* Kathirithamby (Myrmecolacidae), costal margin and wings base.



Figs. 3–4. SEM of strepsipteran metathoracic wings. *Coriophagus rieki* Kinzelbach, costal margins. Note that the costal margin apically bears a single vein (Sc), not the two extended veins (PC+C+ScA and ScP) as drawn by Kukulová-Peck and Lawrence (1993) for this species.



Figs. 5–7. Strepsiptera: Corioxenidae. 5, *Corioxenos* sp. (Mexico) Scale of 0.5 mm.; 6, *Loania* sp. (Panama) Scale of 0.5 mm.; 7, *Dundoxenos* sp. (N. Africa) Scale of 0.2 mm. Venational notation in parenthesis after Kinzelbach (1971) and without parenthesis after Kukalová-Peck and Lawrence (1993). Note that the strepsipteran “pterostigma” (the region between RA_{1+2} and RA_{3+4}) is absent.

Evaluation: This character relies on two distinct morphological features for its definition: the presence of ScP as a discrete vein and its position relative to the pterostigma. We have examined the same strepsipteran taxa surveyed by Kukalová-Peck and Lawrence as well as other Strepsiptera taxa, including the family Corioxenidae. We failed to observe any vein which could possibly equate to the PC+C+ScA as drawn by the authors in the wings of these taxa. Contrary to these drawings, we could not find this vein using scanning electron microscopy (Figs. 1–4) nor using light microscopy (Figs. 8–10). The authors provide no evidence supporting the supposition that this is a vein, and their interpretation relies on the presence of PC+C+ScA and the compliance this interpretation has with the presumed ancestral state. Since PC+C+ScA cannot be distinguished from ScP, it is incorrect to specify a state for ScP and homologize it with the state in Coleoptera. In the Corioxenidae C+Sc splits to Sc which is a single vein without any darkened region posteriorly (Figs. 5–7). In this family, Sc can be clearly distinguished from C but a subdivision of Sc into ScA and ScP is unobservable and the pterostigma is absent (Kathirithamby and Peck, 1994).

Even if the authors feel justified in equating ScP with Sc of Kinzelbach (1971) (in the absence of observing PC+C+ScA), the distribution of this character is problematic. In Strepsiptera, the posterior margin of Sc commonly does not reach the

pterostigma, and in many taxa the pterostigma itself is absent (see character 8 below regarding the strepsipteran "pterostigma").

Character 2: *The apical part of the anterior [wing] margin not strengthened by RA* (Kukalová-Peck and Lawrence 1993; synapomorphy).

Interpretation: The authors provide no criteria for distinguishing a strengthened anterior wing margin from one which is not strengthened. Presumably the states of this character are "strengthened" (plesiomorphy) and "not strengthened" (apomorphy). Until a more precise definition is provided, we cannot evaluate this vague character.

Character 3: *RA and RP diverging abruptly from one another close to the wing base* (Kukalová-Peck and Lawrence, 1993; shared autapomorphic trend).

Interpretation: We presume the states are "not diverging abruptly" (plesiomorphy) and "diverging abruptly" (apomorphy).

Evaluation: The authors present no criterion for what constitutes an abrupt divergence and how it can be distinguished from a non-abrupt divergence. Apparently, there is some angle at which a divergence is abrupt and another at which it is not abrupt, and the two angles do not overlap. If the authors were to argue that the precise angles of divergence (or range of angles) is irrelevant at the ordinal level in insects, then we would likewise counter that this is an irrelevant line of evidence for ordinal level phylogenetic reconstruction. We have observed sufficient variation in the angle of these two veins in Strepsiptera, however, to make us doubt that it can be defined with discrete states (Figs. 5–10). We are further unclear what the authors mean by "shared autapomorphic trend" and how this represents evidence for phylogenetic affinity (discussed below).

Character 4: *Plesiomorphous separation of RA and RP at the wing base* (Kukalová-Peck, 1991; symplesiomorphy?).

Interpretation: The states are apparently "RA and RP basally separate" (plesiomorphy) and "RA and RP basally fused" (apomorphy).

Evaluation: All Strepsiptera and Coleoptera have RA and RP fused basally, as Kukalová-Peck and Lawrence (1993) recognized when they formulated character 3. In the author's "generalized Neopteran wing," these veins are also fused basally. If indeed the separation of RA and RP at the wing base is "plesiomorphous," then how does this symplesiomorphy support the monophyly of Strepsiptera and Coleoptera?

Character 5: *The radial and medial basivenale not fused together into a large plate* (Kukalová-Peck and Lawrence, 1993; shared autapomorphic trend).

Interpretation: The states of this character are presumably "radial and medial basivenale fused" (plesiomorphy) and "radial and basal venale not fused" (apomorphy).

Evaluation: Once again, it is not clear what a shared autapomorphic trend is and how this represents phylogenetic evidence.

Character 6: *RP branches supporting folds* (Kukalová-Peck, 1991; synapomorphy); *the apical field supported by RP branches, which have a somewhat fan-like arrangement* (Kukalová-Peck and Lawrence, 1993; shared autapomorphic trend).

Interpretation: The RP branches are equivalent to Kinzelbach's (1971) R_1 – R_4 . For the first description, the states are apparently "RP branches not supporting folds" (plesiomorphy) and "RP branches supporting folds" (apomorphy). For the second description, the states are "RP branches not supporting apical field, not fan-like"

(plesiomorphy) and “RP branches supporting apical field, somewhat fan-like” (apomorphy).

Evaluation: The authors need to define clearly what constitutes “supporting.” For instance, must RP be directly contiguous to a fold in order to support it or just in the general vicinity of a fold? How far must RP be from a fold before it is considered no longer supporting? Is it possible for a fold to exist in the anterior portion of the wing without coming into contact with RP? The second description assumes that no other insect groups have RP branches in the apical field. The real question, of course, is what is being homologized here. Is it the fact that Strepsiptera and Coleoptera both have folds in the wings? This seems suspect because the system of folds in Coleoptera is quite different from that of Strepsiptera, as the authors have recognized, and we doubt that the folds themselves are homologous. Is the homology implied that only Coleoptera and Strepsiptera have developed a novel way of supporting their folds through the use of RP? This makes the dubious assumption that no other insect has folds that are supported by RP the same way folds are supported in Coleoptera and Strepsiptera. The authors need to clarify what they mean by support and how this type of support is novel to Strepsiptera and Coleoptera.

Character 7: *Reduced CuP* (Kukalová-Peck, 1991; synapomorphy); *CuP reduced* (Kukalová-Peck and Lawrence, 1993; shared autapomorphic trend).

Interpretation: In Kinzelbach’s (1971) drawings of strepsipteran wings CuP is a distinct and often large vein. Kukalová-Peck and Lawrence call this vein AA and treat CuP as either absent or extremely reduced in Strepsiptera. The presumed states of this character are “not reduced” (plesiomorphy) and “reduced” (apomorphy).

Evaluation: In the authors’ drawings of *Mengenilla* sp. and *Coriophagus rieki* (Kukalová-Peck and Lawrence, 1993: figs. 69–70) CuP is absent and in *Lynocholax* (fig. 71) CuP is present as a small vein basally separate from, and apically fused to AA (CuA₂ of Kinzelbach [1971]). In the numerous *Lynocholax* species we have examined, we have not observed this small vein (Fig. 10), nor have we observed such a vein in any strepsipteran taxa. We see no reason why the large posterior vein in Strepsiptera should be considered homologous to AA rather than CuP, and the authors provide no justification for this designation. Hence there is a serious question of homology between the CuP of Coleoptera and what the authors consider the CuP of Strepsiptera.

Character 8: *A shortened RA forming a pterostigma between RA₁₊₂ and RA₃₊₄* (Kukalová-Peck, 1991; synapomorphy).

Interpretation: Kukalová-Peck treats the R₁ of Kinzelbach (1971) basally as RA and distally as RA₁₊₂ and RA₃₊₄, with the darkened region between these branches as a “pterostigma” homologous to the coleopteran pterostigma. It is not clear whether the synapomorphy is a short RA, the formation of a “pterostigma” between RA₁₊₂ and RA₃₊₄, or both. If both, the states are “RA not shortened, RA₁₊₂ and RA₃₊₄ not forming a pterostigma” (plesiomorphy) and “RA short, RA₁₊₂ and RA₃₊₄ forming a pterostigma” (apomorphy).

Evaluation: Kukalová-Peck provides no criteria for distinguishing a shortened RA from a non-shortened RA. The varying lengths of RA we have observed in Strepsiptera, however, make us doubt that it can be defined discretely. The formation of a pigmented pterostigma between RA₁₊₂ and RA₃₊₄ cannot be considered a syna-

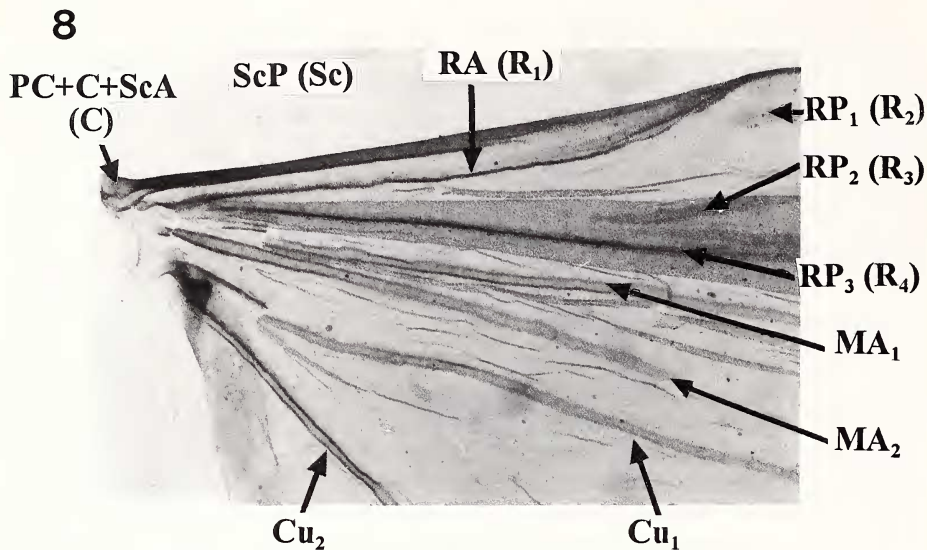


Fig. 8. Light microscope photo of strepsipteran metathoracic wing. Note that RA₁₊₂ is absent in *Mengenilla* and *Coriophagus*. Scale: X35.

pomorphy unique to Strepsiptera and Coleoptera since, as the authors correctly recognize, Hymenoptera and Mecoptera possess this state as well.

We have some reservations with Kukalová-Peck's designation of a pterostigma in Strepsiptera. What she has labelled RA, RA₁₊₂, and RA₃₊₄ is, according to Kinzelbach, a single vein R₁. In some groups of Strepsiptera its distal margins are laterally expanded and the medial region is somewhat sclerotised. In Corioxenidae Sc is distinguishable as a single vein posteriorly (Figs. 5–7) but R₁ is not laterally expanded and this family clearly shows that there is no pterostigma. Furthermore, because Kukalová-Peck and Lawrence (1993) treat the pterostigma as a landmark for homologizing veins (p. 191), they have no criterion for determining whether the pterostigmas themselves are homologous; they simply assume homology.

Character 9: A very long fork of MP (Kukalová-Peck, 1991; synapomorphy).

Interpretation: Kukalová-Peck and Lawrence's drawing (fig. 69) of *Mengenilla* shows MP forked into MP₁₊₂ (MA₁ of Kinzelbach) and MP₃₊₄ (MA₂ of Kinzelbach). The states of this character are "fork not very long" (plesiomorphy) and "fork very long" (apomorphy).

Evaluation: The authors provide no criterion for distinguishing a "very long" fork from one which is "not very long." We have examined all the genera of the most basal Strepsiptera, the Mengenillidae (*Mengenilla*, *Eoxenos*, and a new genus from N. Africa [Kathirithamby, in prep.]). Contrary to the author's drawings, in all of these taxa MP is not forked (i.e., MA₁ and MA₂ are not joined basally, Fig. 8).

CRITIQUE OF PHYLOGENETIC METHODOLOGY

While the authors couch their terminology in cladistic parlance, their methodology is pseudo-cladistic and at discord with the theoretical basis of cladistics. The authors

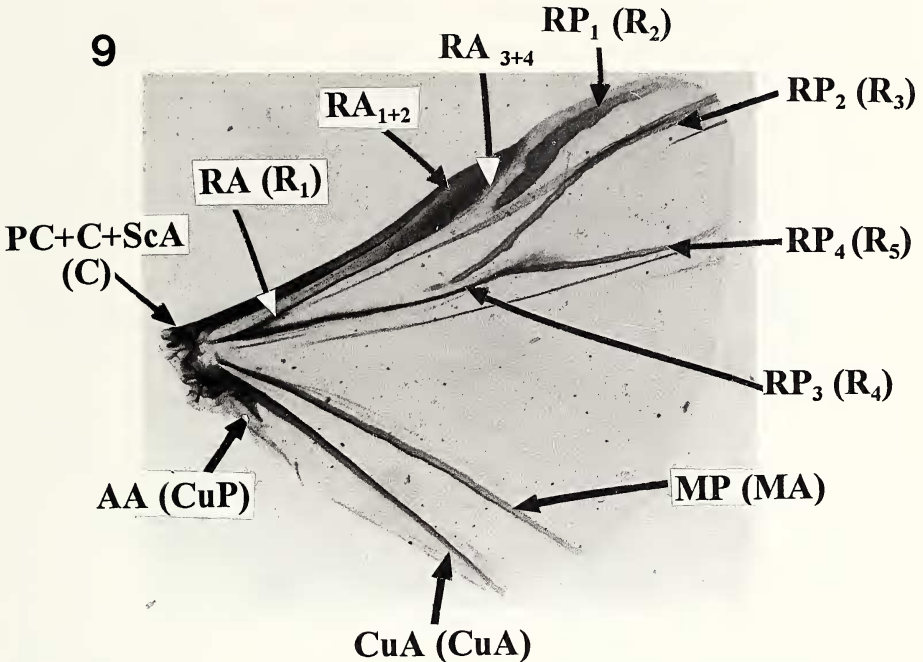


Fig. 9. Light microscopic photo of strepsipteran metathoracic wing. *Coriophagus rieki* Kinzelbach (Halictophagidae). Scale: X26.

do not follow cladistic principles in selecting characters, determining character polarity, appealing unduly to groundplans and evolutionary scenarios, neglecting a formal parsimony analysis prior to their conclusions, and using “shared autapomorphic trends” to support monophyly.

Rooting and polarity

The authors do not follow the application of character polarity in a cladistic context. Character polarity is assessed by outgroup comparison or ontogenetic study and is determined directly by where the root is placed in a branching network (Waltros and Wheeler, 1981; Farris, 1982; see Nixon and Carpenter [1993] for an excellent discussion). Character states are scored for the ingroup and outgroup taxa, an unrooted network is generated, the ingroup is rooted to the outgroup, and the polarity of the characters are subsequently obtained by their optimization on the tree. There is no need—and indeed, no clear way—to establish whether a character is “primitive” or “derived” prior to cladistic analysis (Nixon and Carpenter, 1993). Neither is there any need for scenarios involving the direction a suite of characters must have evolved in order for the characters to be phylogenetically informative. The distinction between synapomorphy and plesiomorphy is meaningless in the absence of a rooted cladogram, and the assignment of polarity in the absence of a tree is specious.

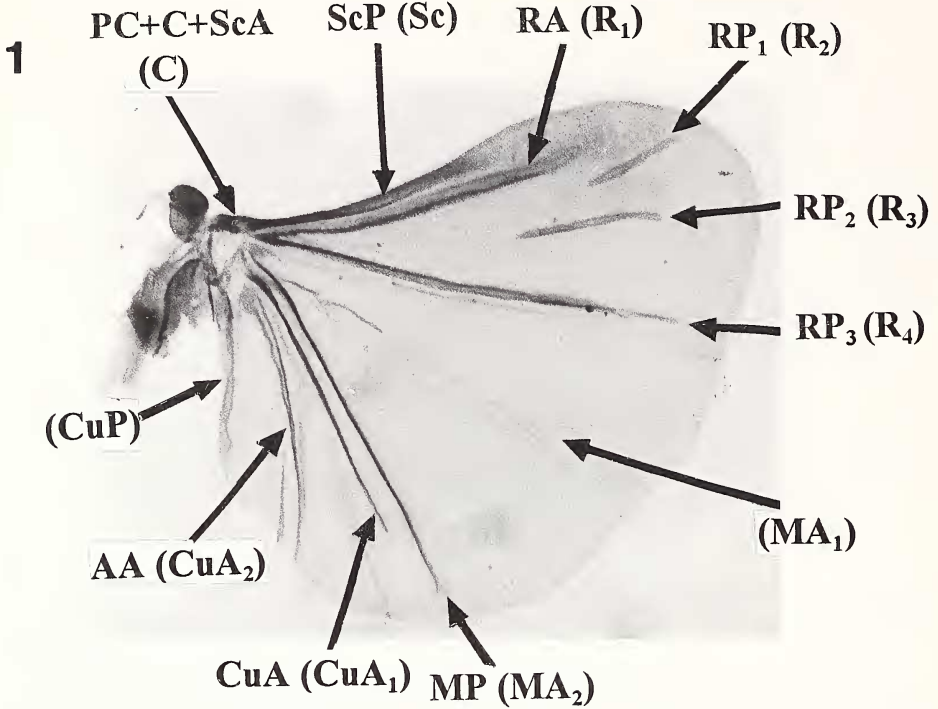


Fig. 10. Light microscopic photo of strepsipteran metathoracic wing. *Lychnocolax drysdalensis* Kathirithamby (Myrmecolacidae). Scale: X54.

The polarization of the venational characters presented by Kukalová-Peck and Lawrence is not based on any empirical evidence of character state distribution in ingroups and outgroups. Instead, the authors rely on comparisons to the “all-apterygote groundplan” and appeals to scenarios of directionality in the evolution of insect veins. How are these groundplans generated? “Venational groundplan is a *compilation of primitive features* [sic] assembled over many years by comparing the primitive representatives of *all* [sic] extinct and extant pterygote orders” (Kukalová-Peck and Lawrence, 1993: 194). The authors’ designations of character polarities are simple statements of concordance with some preconceived notion of primitive wing venation; this is a far cry from polarization as it is commonly practiced in cladistic analysis.

Beyond the sheer subjectivity of this methodology, and the rather dubious claim that all extinct insect orders have left traces for these authors to include in their groundplan, we find a number of problems with this procedure. First of all, organisms are not compilations of distinct features found in different groups (if so, phylogenetics would be a meaningless pursuit). By the authors’ own admission, there has never been an organism observed which possesses all of these putatively primitive wing features in combination. Then why should the combination of character states observed in extant (or extinct) taxa be polarized by comparing them with a combi-

nation of states which has never been observed in any taxon? How can unobserved states in a hypothetical taxon constitute evidence for polarization? Why should presumed data (which are not really data anyway) take precedence over observable data?

In the authors' explanation of the groundplan, they suggest that the groundplan represents the primitive states of characters as found in the most recent common ancestor of all the taxa used in the compilation. But how is this combination of presumed ancestral states obtained? It is clearly **not** obtained by the cladistic practice of optimizing characters on nodes of a cladogram. It is in fact quite possible that the combination of character states as proposed for the "all-pterygote" ancestor cannot co-occur once those states are optimized on a tree. Moreover, why would we expect the common ancestor of those taxa to have all the presumably primitive features of all the taxa used in the compilation? This would seem to suggest that all the taxa share only that ancestor in common rather than sharing a hierarchy of ancestry.

More critically, how do the authors know that these states are indeed primitive? This tautological conclusion stems from the procedure of using "primitive representatives" to infer "primitive features". How do we know these representatives are primitive? Simple, they have retained primitive features. How do we know they have retained primitive features? Because they are primitive taxa. But of course whether they are *a priori* considered primitive or not is moot for cladistic analysis. The real question should be how do the authors know, in the absence of a cladogram, that a given character is a synapomorphy? Once more, the authors are confronted with drawing conclusions of polarity without reference to a specific phylogeny.

This confusion over cladistic methodology is best summarized by the authors' statement that "it is also not possible [to use coleopteran venation in phylogeny] without determining the succession of veinal character states based on the all-pterygote groundplan" (p. 194). It is possible and, in fact, is routine to use venational characters for phylogenetic inference by scoring similar vein modifications in multiple taxa and appropriate outgroups without reference to a groundplan. A tree is reconstructed, a rooting selected, and then (if one wishes) the "succession of veinal character states" can be hypothesized by the optimization of these characters on the tree. It is not that we are specifically arguing that this groundplan is incorrect, we are only arguing that the groundplan has not been inferred correctly and that it should not be used as a means to polarize characters. The use of artificial amalgamations of presumed primitive characters as a basis for character polarization is without theoretical and empirical support and is far outside the realm of cladistic analysis.

Outgroups and analysis

We are concerned with the authors' apparent lack of adequate comparison of their putative synapomorphies with the appropriate outgroups. These characters were not explicitly scored for other holometabolous insect orders, nor were they specifically scored for the Paraneoptera which are the currently accepted outgroup to the Holometabola (Kristensen, 1991). Because the authors have presented us with only a two taxon statement, we have no way of knowing the level of generality of these characters. It appears that the authors assumed *a priori* that Strepsiptera and Coleoptera

are sister-groups, thereby forcing a coleopteran venational scheme upon Strepsiptera, and they then searched for characters which would validate this supposition.

The authors also did not provide a specific cladistic analysis of their character data in the Strepsiptera, Coleoptera, and outgroups. In the absence of this analysis, it is premature for the authors to make any claims regarding whether a character is a synapomorphy or not. Hence, even if the authors' putative synapomorphies could be defined as discrete characters, they have yet to demonstrate in an analysis that any of these shared similarities are unique to Strepsiptera and Coleoptera and are synapomorphic rather than symplesiomorphic. The conclusion that a particular character is a synapomorphy, with no explicit cladistic analysis to determine polarity, smacks more of authoritarianism than science.

Evolutionary scenarios

The success of cladistics has lain in part with its ability to separate pattern and process: phylogenies represent the pattern from which evolutionary processes are inferred. Thus cladistics attempts to tease apart the evidence for phylogeny from any specific model of evolution (Eldredge and Cracraft, 1980).

The authors have unduly mixed pattern with process into their phylogenetic conclusions by proceeding under the assumption that veins evolve according to a known set of rules and that character designation and polarity determination can be confidently based upon these rules. These rules include the "two major venational principles": (1) the loss of primary veins and their main branches is irreversible, and (2) the fusion of two primary veins near the wing base is irreversible. According to the authors, the veracity of these principles is established by the fact that entomologists have been studying veins for over 100 years and that "through this long experience, the sequences of character change have become well established" (Kukalová-Peck and Lawrence, 1993: 186). We are not so confident. It is not clear to us why the authors consider these principles well established as they have never been empirically tested on a phylogeny created independent of these principles. As no one (to our knowledge) has used parsimony to optimize the fusion and loss of primary veins on an ordinal phylogeny for the insects and demonstrated evolution according to Dollo parsimony, we would argue that there yet remains no specific test for the veracity of these principles.

Our argument is not that these principles are wrong, only that the authors have placed undue weight on their veracity in drawing phylogenetic conclusions. These principles may be true. But because the authors have needlessly based their phylogenetic conclusions on these assumptions, they cannot specifically test these principles using their phylogeny.

Autapomorphic trends

The authors appear confused as to what types of characters constitute evidence for phylogenetic inference—is it synapomorphy, symplesiomorphy (character 4), or "shared autapomorphic trends" (characters 3, 5, 6, & 7)? The use of the term "shared autapomorphic trend" is not derived from cladistic literature. How is a shared autapomorphic trend indicative of phylogeny? In what sense is a shared autapomorphic trend a derived homologous feature in a group of organisms? If a trend

is shared, what is the level of generality of this sharing? How does sharing a trend translate to a unique, derived evolutionary event in the common lineage of these presumed sister-taxa? How does one in practice distinguish a shared autapomorphic trend from a synapomorphy?

The author's claim that certain characters constitute autapomorphic trends seems to indicate they think them weaker than a synapomorphy, but still phylogenetically informative. This may explain why characters 6 and 7 were changed (without explanation) from synapomorphies in the 1991 paper to shared autapomorphic trends in the 1993 paper. The notion that shared autapomorphic trends are phylogenetically informative, however, is dangerous in that it allows **any** character distribution to be interpreted as synapomorphic evidence. The concept of shared autapomorphic trends as indicative of phylogeny is foreign to cladistic theory.

CONCLUSIONS

Venational homologies in the highly modified hind wings of Coleoptera have long eluded entomologists. The attempt by Kukulová-Peck and Lawrence is a commendable effort, but we have some basic criticisms of their character interpretations and phylogenetic methodology.

As detailed above, we are concerned with the author's misinterpretation of strepsipteran morphology. The characters they have proposed are in many cases unobservable, continuous, or of questionable homology. We have further demonstrated discrepancy between the veins the authors have drawn on the three strepsipteran species they examined, and those which we observe in the specimens. Kukulová-Peck (1991) concludes that "quite clearly, Strepsiptera venation can be derived only from a common ancestor with Coleoptera or from a coleopteroid stem group" (p. 178). We argue that their current analysis does not support this conclusion.

By failing to score these characters in other holometabolous insect orders and neglecting to score any other venational character which Strepsiptera (or Coleoptera) may share with any other insect order, Kukulová-Peck and Lawrence have biased their results to support their conclusions. We feel that the authors should be more concerned with scoring putatively homologous venational features across multiple ingroup and outgroup taxa, creating a character matrix with these and other characters for a formal cladistic analysis, and allow parsimony to arbitrate among possible phylogenetic conclusions and to decide which characters are synapomorphies. The hypothetical ancestral states can then be derived by optimizing the venational states on the tree and any scenario for trends in venational evolution could likewise be derived from the tree. The characters lead to the presumed ancestral states and not the presumed ancestral states to the characters.

We find no evidence from the hind wing venation to support a sister-group relationship between Strepsiptera and Coleoptera.

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